STUDIES ON AUSTRALIAN THYNNIDAE SHUCKARD, 1841. (HYMENOPTERA) III.

An Introduction to the Comparative Morphology of the Male.

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(Thirty-one Text-figures.)

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Synopsis.

The present paper is essentially introductory; it precedes a revision of the family and summarizes the various modifications found in the principal regions of the body of male thynnids. It contains four tables and thirty-one illustrations representing the taxonomic characters selected by earlier workers to distinguish the genera. The type species were used mostly for these figures and with graphic redefinition it is hoped to verify much of the existing classification and to clarify some of the ambiguities occurring in the former generic key.

Introduction.

This morphological study follows directly from the catalogue and history of Thynnidae already published. It is the third in this introductory series and deals with the comparative anatomy of the males of the Australian species. Together, these three papers summarize the contributions made during a hundred and eighty years by fifty naturalists. The volume of information on the Australian Thynnidae is very considerable. Previously, no attempt has been made to compile a list of the various regions of the body which are subject to modification, and a complete investigation of these variants forms part of the revision that is now in progress. However, before proceeding with this revision it is appropriate here to bring together the salient features of thynnid anatomy.

Accounts of earlier achievements have become a traditional introduction, and we find that the contributions of Guérin-Méneville (1838), Klug (1842) and Westwood (1844) were each prefaced by a résumé of the works of their predecessors. The genera and species already described prior to 1859 were listed in Smith's first catalogue, and a brief history of foregoing research introduces Rowland Turner's revision. Following precedent, therefore, the checklist (1954), history (1956) and now this morphological study sum up our present knowledge of the Thynnidae. That there is a great deal of information available on thynnid morphology is true, but to accept unverified the statements made by preceding authors on this subject has proved impossible. A classical example of such folly is found in early thynnid history. Latreille (1809), in presenting his observations on the specimens of *Thynnus dentatus*, which of course were all winged males, gave his imaginary characters to distinguish, as he thought, males from females. Then, as the reprinting of former observations was customary between 1775 and 1825, Latreille's errors were duplicated again both by Lamarck (1817) and Lepeletier (1825).

The present paper is not simply a concise summary of all the earlier works on this subject; it is considerably more than that. Here the papers written by Turner and others have been submitted to critical examination and their statements checked and compared with identified material. One of its primary objectives is to investigate the taxonomic characters contrasted by Turner in the couplets in his generic key (1910), as this key contains certain sections in which the taxonomic characters given are inadequately described, and many of his statements are ambiguous.

The salient features by which each genus was defined have been carefully examined and a series of illustrations made of the characters used to distinguish one genus from another. The type species of each genus was used in most cases. With Turner's key interpreted by precise, accurately drawn figures demonstrating the generic definitions, recognition of many of the genera should be considerably simplified. Furthermore, as the species are at present arranged, a certain number do not agree with the taxonomic characters of the genera into which they have been grouped by Turner, and in some cases it appears doubtful whether Turner has arranged his species in accordance with the characters defined by him in his own generic key. Thus to take this investigation further, it will eventually be necessary for every species to be checked with the typical example of each genus, as it is certain that many of the species listed are incorrectly classified. The illustrations submitted in the present paper are intended to act as "blueprints" for the subsequent verification of the genera in which the 480 species are supposed to have been classified. It is anticipated that the study of the genitalia of these insects will later prove of considerable importance in interpreting the classification, phylogeny and certain evolutionary lines which suggest themselves from a study of Thynnidae. An examination of 2000 of these structures is now in progress.

Instead of figures, Turner's work has in some cases been tested by means of measurements and the results are tabulated, although the samples employed are insufficiently large to be of real significance.

With a family of such a size as the Thynnidae, the amount of detailed information to be compiled on all of its species will be immense. For further reference, the coding and filing of the details of each species appropriately into a punch-card system is an essential. The present paper is an attempt to provide a working basis for this subsequent investigation. It is hoped also that this contribution will bring about some uniformity in the subsequent redescription of the genera and species which must eventually follow.

To be consistent in the use of taxonomic categories is more than desirable, and as views differ in regard to the category to be applied to the thynnids it is appropriate here to quote the definition given by Mayr (1953) of the category—Family: "A family may be defined as a systematic category including one genus or a group of genera of common phylogenetic origin, which is separated from other families by a decided gap. As for the genus, it is suggested that the size of the gap be in inverse ratio to the size of the family." If Mayr's definition is accepted, it follows that since the group is of very large size, then, even if the gap which separates the thynnids from their allies is but small, the category—family—logically follows from his definition. An assessment of the extent of this gap obviously depends upon further studies of their comparative anatomy.

In the *Genera Insectorum* 1910, Turner set out the generic descriptions for every genus and also the type species selected to represent each genus. It would be expected that the generic descriptions apply fairly closely to these type species, and as the present paper deals largely with generic characters, a list follows of the type species of the genera.

LIST OF THE TYPE SPECIES OF THE GENERA OF THE THYNNIDAE. SHUCKARD, 1841.

Subfamily DIAMMINAE Turner, 1907.

Diamma bicolor Westwood, 1835.

Subfamily RHAGIGASTERINAE Ashmead, 1903.

Dimorphothynnus bicolor (Westwood), 1844.
Eirone dispar Westwood, 1844.
Rhagigaster unicolor Guérin, 1838.

Subfamily THYNNINAE Ashmead, 1903.

Ariphron bicolor Erichson, 1842.
Tachynomyia abdominalis (Guérin), 1842.
Megalothynnus klugii (Westwood), 1844.
Oncorhinothynnus xanthospilus (Shuckard), 1841.
Psammothynnus depressus (Westwood), 1844.
Phymatothynnus monilicornis (Smith), 1859.
Zeleboria xanthorrhoei (Smith), 1859.
Aulacothynnus femoratus (Turner), 1908.
Neozeleboria sexmaculata (Smith), 1859.
Agriomyia maculata Guérin, 1838.
Asthenothynnus pulchellus (Klug), 1842.
Leiothynnus mackayensis Turner, 1908.
Aspidothynnus combustus (Smith), 1859.
Gymnothynnus gilberti Turner, 1908.
Epactiothynnus crabroniformis (Smith), 1859.
Tmesothynnus zelebori (Saussure), 1868.
Thynnoturneria cerceroides (Smith), 1859.

Subfamily THYNNINAE Ashmead, 1903 (continued).

Acanthothynnus sannae (Turner), 1908.
Doratithynnus doddii (Turner), 1908.
Encopothynnus spinulosus Turner, 1915.
Catocheilus klugii Guérin, 1842.
Hemithynnus apterus (Olivier), 1811.
Lophocheilus villosus Guérin, 1842.
Macrothynnus simillimus (Smith), 1859.
Thynnoides fulvipes Guérin, 1838.
Elidothynnus melleus (Westwood), 1844.
Campylothynnus flavopictus (Smith), 1859.
Lestricothynnus nubilipennis (Smith), 1879.
Belothynnus unifasciatus (Smith), 1873.
Leptothynnus purpureipennis (Westwood), 1844.
Guerinius flavilabris (Guérin), 1842.
Pogonothynnus fenestratus (Smith), 1859.
Zaspilothynnus leachiellus (Westwood), 1844.
Thynnus dentatus Fabricius, 1775.
Iswaroides koebelei Ashmead, 1899.

SUMMARY.

An illustrated account is given of the morphology of the head, thorax, abdomen and their several sclerites and appendages. Special reference is made to selected taxonomic characters as an aid to subsequent studies on Australian Thynnidae. There is a general tendency in thynnids for small ridges, crests and spines to arise on various portions of the body, especially on the frons, pronotum, anterior coxae, posterior femora, abdominal segments and hypopygium. Particular attention has been given to the features listed as follows:

The Head: 1. The frons; frontal ridges. 2. The clypeus; epistomal suture, inter-antennal bridge; (*a*) dimensions of the median axis, (*b*) apex of the clypeus, (*c*) median clypeal protuberance. 3. The occipital region; pollen pouch, occipital suture, hypostomal bridge. 4. The antennae; (*a*) length, (*b*) diameter at base and apex, (*c*) segments. 5. The maxillary palp and relative length of segments.

The Thorax: 1. Regions: pronotum, mesepisternum, scutellum and propodaeum. 2. Legs; (*a*) anterior coxae, (*b*) the second pair of coxae and the mesosternum, (*c*) the posterior femora. 3. Fore-wing and venation.

The Abdomen: (*a*) The shape of the abdomen; (*b*) the moulding of the abdominal segments; (*c*) the abdominal protuberances—median tubercle, projections borne by the postero-lateral aspect of certain segments and dorsal ornamentation; (*d*) the pygidium; and (*e*) the hypopygium.

Many of the characters which Turner contrasts in his couplets intergrade to such an extent that their value in taxonomy is most doubtful, and it is only in species where the generic characters are reasonably well developed that any certainty exists in their arrangement into genera. Consequently, the determination of the systematic position of many species is impossible until investigations in this group have been further advanced.

Acknowledgements.

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COMPARATIVE MORPHOLOGY OF THE MALE.

Shape and Size.

The general shape of the male in thynnids varies from stout, robust, thickset forms, to examples which are elongate and very slightly built. As regards their size there is considerable latitude; the largest known examples are *Megalothynnus klugii* (Westwood) and *M. poultoni* (Turner), which are 35 mm. and 36 mm. respectively, while the smallest species available to the present author measures 4·5 mm. and has not yet been identified. In many species the size of the males is variable; for example, in *Oncorhinothynnus xanthospilus* (Shuckard) the size ranges from a maximum of 2·7 cm. to a minimum of 1·8 cm.

The Head.

In these insects much interest centres in the head and the form of several of its sclerites and appendages. There are typical frontal ridges which are characteristic of all Thynnidae, while modifications occur in the structure of the clypeal, postgenal and occipital regions, as well as in the form of the antenna and maxillary palp. The morphology of the head and the anatomy of the tentoria can best be examined in specimens which have been cleared in caustic alkali; however, without adequate supplies of material, this is not always practicable. For convenience, therefore, the illustrations in the present paper have been drawn from pinned specimens.

TABLE 1.

Dimensions of the Clypeus.

" Clypeus long " characterized *Aspidothynnus* in contrast to *Epactiothynnus* and *Tmesothynnus* in which the clypeus is said to be " short ". Actual lengths are tabulated and for comparative purposes related to the dimensions of the transverse axis. The ratio is expressed as a percentage.

Species.	Dimensions of Median and Transverse Axes of Clypeus.		Ratio of Median to Transverse Axis Expressed as a Percentage.	Taxonomic Character Implied by Turner in Generic Key of 1910.
	Median Axis.	Transverse Axis.		
	mm.	mm.	%	
Epactiothynnus excellens	0·54	1·38	39	" Clypeus short."
Epactiothynnus jardini	0·62	1·26	41	,, ,,
Tmesothynnus zelebori	0·68	1·5	46	,, ,,
Epactiothynnus crabroniformis	0·86	1·51	53	,, ,,
Aspidothynnus fossulatus	0·78	1·13	70	" Clypeus long."

1. *The Frons.*

The frons was not mentioned by Turner in his generic key to the Thynnidae, but it has, however, a special significance. In the Thynnidae and Myzinidae the antennae arise from beneath frontal ridges or tubercles, contrasting with the Tiphiidae and the Anthoboscidae,* in which the antennae arise from sockets with simple reflexed rims and not from beneath frontal ridges or tubercles (Pate, 1947). On the vertex there are three ocelli.

2. *The Clypeus.*

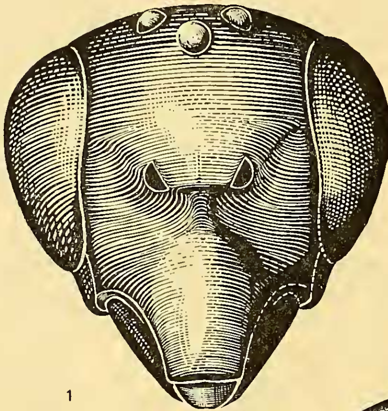
Both the peripheral region of the clypeus and the moulding of its median axis are subject to modification. Firstly, appreciable differences can be recognized in (*a*) the relative dimensions of the median to transverse axes, and (*b*) the width of the apex of the clypeus compared with its base. Secondly, the clypeus in very many thynnids bears a median protuberance which is variable in contour.

Thynnid morphology has not yet been adequately described, thus the limits of the clypeus in this family have never been defined. The *epistomal suture*, separating clypeus from frons, arises near the junction of the eyes and genae to cross over the narrow inter-antennal bridge which unites the clypeal protuberance with the frontal ridges. There are species, such as *Agriomyia trochanterina* (Westwood) in which the

* Anthoboscidae: *Anthobosca australasiae* Guérin, 1838, Port Jackson (Atlas, 1830, T. 8, f. 8), was the first described representative of this family. Its distribution is southern; there are thirty-seven Australian, seventeen Ethiopian and eleven South American species (Pate, 1947). This family was considered by Turner (1907), (1912), and later by Tillyard (1926), to be part of the Scoliidae.

epistomal suture is plainly visible in pinned specimens, but in many others it is preferable to work from cleared heads in order that this suture may be fully displayed.

In forms in which the suture is indistinct, measurements of the length of the median longitudinal axis were made from the clypeal apex to the centre of the inter-antennal bridge. So that the length of the clypeus could be compared in different species of the Thynnidae, the length of the median axis is related to the



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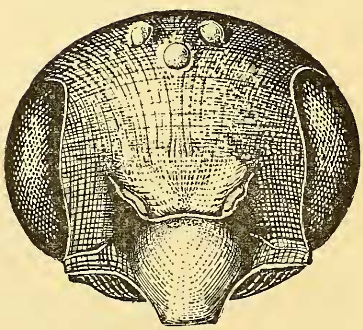

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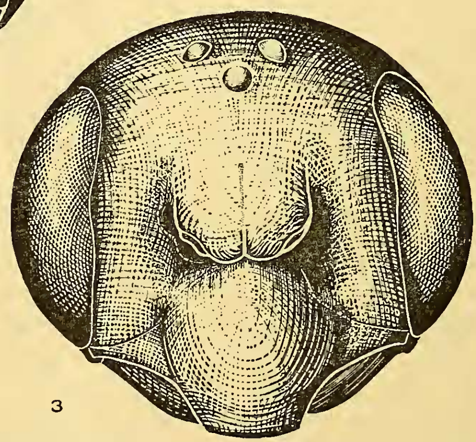

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Text-fig. 1.—Head of *Aspidothynnus fossulatus* Turner illustrating Turner's character "clypeus long". It also illustrates the moulding of the clypeus, the inter-antennal bridge, the antennae arising beneath frontal ridges, the genae, labrum, and the three ocelli.

Text-fig. 2.—Head of *Asthenothynnus pulchellus* (Klug) illustrating Turner's "clypeus very narrowly truncate at apex".

Text-fig. 3.—Head of *Leiothynnus mackayensis* Turner; to show what is meant by the contrasted character "clypeus more broadly truncate".

(It is to be noted that in both these illustrations (Text-figs. 2, 3) there is an obvious median clypeal protuberance and consequently neither of these species agrees with the taxonomic character which was set down by Turner in his 1910 key.)

dimensions of the transverse axis, thus providing a basis for inter-specific comparison. The transverse dimension of the clypeus was taken as the entire width of its oral margin and the ratio of medial to transverse axes is expressed as a percentage.

(*a*) *The dimensions of the median axis.*

The length of the median axis of the clypeus refers in particular to *Aspidothynnus* Turner (Text-fig. 1). The taxonomic character coined by Turner, "clypeus long", is supposed to separate the four species of *Aspidothynnus* from its converse, "clypeus short", which presumably should apply to all the thirty-four species grouped in the genera *Gymnothynnus* Turner, *Epactiothynnus* Turner and *Tmesothynnus* Turner.

(*b*) *The apex of the clypeus.*

The taxonomic characters in Turner's key, reading "clypeus broad at the apex *Glaphyrothynnus*", separates *Zeleboria* Saussure (Text-fig. 4) from "clypeus narrow at the apex, not large", which is characteristic of *Psammothynnus* Ashmead (Text-fig. 5), *Phymatothynnus* Turner (Text-fig. 6), *Neozeleboria* Rohwer, *Asthenothynnus* Turner (Text-fig. 2) and *Leiothynnus* Turner (Text-fig. 3).

Grouped in this taxonomic character, "clypeus narrow at the apex", are the genera *Leiothynnus* and *Asthenothynnus*. The couplet given for their separation reads: "clypeus very narrowly truncate at the apex" *Asthenothynnus* and "clypeus more broadly truncate" *Leiothynnus*.

Illustrations are given in Text-figures 2 and 3, and an analysis of Turner's observations by actual measurements of the clypeus is set out in Table 2. The

TABLE 2.

The Dimensions of the Clypeus at the Apex and Base.

As a taxonomic character, the relative width of the clypeus was used by Turner and an attempt is made here to estimate the value of such comparisons as " clypeus broad ", " narrow " and " very narrow ". For the species listed in this table, apical and basal dimensions are given, and in order to simplify inter-specific comparison, the ratio of the apex to the base is expressed as a percentage. The species marked with an asterisk are type species.

Species.	Dimensions of Clypeus at		Ratio of Apical to Basal Dimensions Expressed as a Percentage.	Taxonomic Character Implied by Turner in Generic Key of 1910.
	Apex.	Base.		
	mm.	mm.	%	
Asthenothynnus decoratus	0·16	1·02	16	" Clypeus very narrowly truncate at apex."
*Asthenothynnus pulchellus**	0·25	1·12	22	,, ,, ,, ,,
*Asthenothynnus pulchellus**	0·28	1·12	25	,, ,, ,, ,,
Phymatothynnus nitidus	0·42	1·69	25	" Clypeus narrow at apex, not large."
Asthenothynnus maritimus	0·31	1·15	27	" Clypeus very narrowly truncate at apex."
*Psammothynnus depressus**	0·43	1·59	27	" Clypeus narrow at apex, not large."
*Neozeleboria sexmaculata**	0·59	2·13	28	,, ,, ,, ,,
*Aulacothynnus femoratus**	0·43	1·5	29	,, ,, ,, ,,
*Leiothynnus mackayensis**	0·51	1·44	35	" Clypeus more broadly truncate."
Zeleboria marginalis	0·72	1·77	41	" Clypeus large, broad at apex."
Zeleboria carinata	0·78	1·83	43	,, ,, ,,
*Zeleboria xanthorrhoei**	0·81	1·66	49	,, ,, ,,

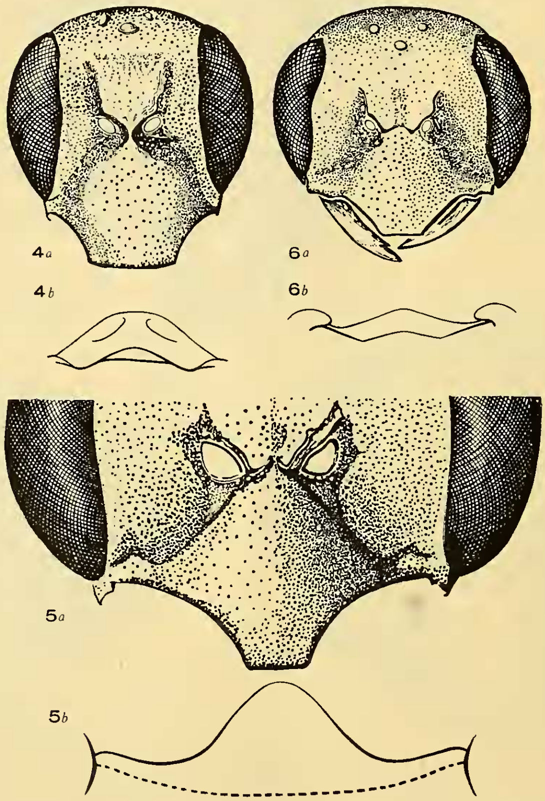
dimensions of the apex of the clypeus are given for a dozen species and, for comparison, are related to the transverse dimensions of the clypeus at its base. In order that the dimensions of the apex of the clypeus may be compared in different species, the ratio of the width of the apex to base is expressed as a percentage.

As an example of the discrepancies which appear in Turner's writings, we find that of the sixty-one species included in the six genera *Psammothynnus*, *Phymatothynnus*, *Neozeleboria*, *Aulacothynnus*, *Asthenothynnus* and *Leiothynnus* there are at least nine descriptions given in which Turner deliberately contradicts his chosen taxonomic character: "clypeus narrow at the apex". Thus there are at least 15% of the species in this group which disagree with his definition as stated in the generic key of 1910. These species are *Asthenothynnus innocuus*, *Psammothynnus kershawi*, *Psammothynnus rubricans*, *Phymatothynnus pygidialis*, *Neozeleboria ada*, *Neozeleboria alexandri*, *Neozeleboria carinicollis*, *Neozeleboria proxima*, and lastly, according to the descriptions given by Turner, even the type species *Neozeleboria sexmaculata*, selected by him to represent that genus, fails to conform to the prescribed taxonomic character on which the genus was defined. Comparative widths of the apex were also used by

Turner to separate the twenty-one species of *Epactiothynnus* from the several species in his genus *Gymnothynnus*, but it is difficult to interpret this section of his key.

(*c*) *The median clypeal protuberance.*

The clypeus in many thynnids bears a median protuberance which is variously modified. To Turner, the structure was known as a median carina, but as it is not necessarily shaped like a keel, median protuberance is a preferable term. There are three forms of median protuberance: (i) subspherical, (ii) carinate, and (iii) non-carinate. The first example attains maximum development in *Zeleboria* Saussure,



Text-fig. 4.—*Zeleboria xanthorrhoei* (Smith). (*a*) Head to illustrate Turner's character—"clypeus large, convex, broad at the apex, with a median carina". (*b*) Head from apical aspect to show shape of carina.

Text-fig. 5.—*Psammothynnus depressus* (Westwood). (*a*) Head illustrating Turner's statement—"clypeus with carina". (*b*) Head from apical aspect to show shape of carina; in this figure the apex of the clypeus is obscured by the mandibles and their upper edges are indicated by a broken line.

Text-fig. 6.—*Phymatothynnus nitidus* (Smith). (*a*) Head illustrating Turner's statement—"clypeus without carina". (*b*) Head from apical aspect to show shape of carina.

and in this genus it is predominantly rounded and subspherical. The second type of protuberance is distinctly ridge shaped; it consists of two planes meeting along the medial axis, thus giving rise to a gable-like structure as in roofing, which can appropriately be called carinate, as it bears a resemblance to a keel. Such an example is *Psammothynnus depressus* (Westwood). In the third instance there are five associated genera defined by Turner in his key as "without a carina", and here the median protuberance is not so strongly accentuated, but none the less a carina still occurs. These three examples of clypeal modifications are illustrated by *Zeleboria* *xanthorrhoei* (Text-fig. 4), *Psammothynnus depressus* (Text-fig. 5) and *Phymatothynnus nitidus* (Text-fig. 6).

(i) *The subspherical protuberance.*—This type of protuberance occurring in *Zeleboria* (Text-fig. 4) shows the maximum degree of development. Here the clypeus is extended to form a large, convex dome which occupies its whole surface. Its convex nature had, in fact, been selected by Ashmead (1903) in redescribing Saussure's genus. The descriptions given of the nine species in this genus all agree regarding the inflated form of the protuberance, and its subspherical shape does not always resemble a keel as the term carina would suggest.

It is worth noting here that *Thynnus carinatus* Smith was selected by Henri de Saussure as the type species for his genus *Zeleboria*, and that Turner, disregarding the rules of nomenclature, transferred *Zeleboria carinata* (Smith), together with *Thynnus xanthorrhoei* Smith, to his new genus *Glaphyrothynnus* Turner, 1910, and made *G. xanthorrhoei* the type species of his genus. But since *Zeleboria* was tied by Saussure to *Zeleboria carinata* in 1867, the inclusion of this species in *Glaphyrothynnus* Turner, 1910, meant that Turner had only proposed *Glaphyrothynnus* as another name for an existing genus. Saussure's comment on this species reads: "ausser dass der Clypeus wie bei *Thynnus* gebildet . . .", and also: "dass der Kiel des Clypeus sich bis am Vorderrand erstreckt;".

(ii) *The carinate protuberance.*—The presence of this ridge was utilized by Turner to separate the genus *Psammothynnus*, in which a carina occurs, from *Phymatothynnus* Turner, *Aulacothynnus* Turner, *Neozeleboria* Rohwer, *Asthenothynnus* Turner and *Leiothynnus* Turner, in which such a carina is said by him to be absent. The presence of a carina in the five species of *Psammothynnus* is supposed to distinguish them from a total of fifty-four species included in the genera listed above. In refuting Turner's statement, attention is directed to *Asthenothynnus pulchellus* (Text-fig. 2) and *Leiothynnus mackayensis* (Text-fig. 3), in which a well-developed carina is clearly shown.

Unfortunately, it is found once more that Turner's descriptions of the species in these genera conflict with his generic characters. Turner stated in the key that the clypeus was without a carina in the foregoing genera; while in describing twelve of the fifty-four species concerned he clearly stated that there is a carina present on the clypeus. Thus at least 22% of his descriptions do not conform to the taxonomic characters which he had previously stipulated in the generic key. These species are: *Phymatothynnus derelictus*, *Phymatothynnus pygidialis*, *Phymatothynnus pygidiophorus*, *Phymatothynnus zenis*, *Phymatothynnus nitidus*, *Neozeleboria polita*, *Asthenothynnus beatrix*, *Asthenothynnus innocuus*, *Asthenothynnus penetrans*, *Asthenothynnus pygmaeus*, *Asthenothynnus rubromaculatus* and *Asthenothynnus vicarius*.

(iii) *Clypeus with reduced carina.*—The genera concerned, if we were to accept Turner's key literally, are *Phymatothynnus*, *Aulacothynnus*, *Neozeleboria*, *Asthenothynnus* and *Leiothynnus*, but a flat clypeus devoid of any carina apparently was never implied here by him. On the contrary, examination of such examples as *Asthenothynnus pulchellus* (Klug) (Text-fig. 2), *Phymatothynnus nitidus* Smith (Text-fig. 6) and *Leiothynnus mackayensis* Turner (Text-fig. 3) shows that the median protuberance is present and well developed, despite his taxonomic character given in the generic key. An attempt to show the nature of this median protuberance in *Phymatothynnus nitidus* is made in Text-fig. 6.

3. *The Occipital Region.*

The head in thynnids is concave on the ventral surface and within this concavity the neck is received. This concavity reaches its maximum development in *Tachynomyia* Guérin (Text-fig. 7), and here the genae are expanded and heavily fringed with long hairs. In *Tachynomyia* a saucer-like cavity is formed which serves as a pouch in which pollen and nectar are stored, and in some pinned specimens this pouch may still contain dried pollen. Turner used this structure as a taxonomic character to separate *Tachynomyia* from other genera and his key reads: "head very strongly hollowed beneath, with a fringe of long recurved hairs on the sides". Unfortunately *Megalo-*

thynnus Turner was bracketed with this genus; however, there is no phylogenetic relationship between them and the occipital cavity present in this giant thynnid is relatively no greater than it is in other genera.

The occipital concavity appears to be bounded by the *occipital suture* and its invaginated fold or ridge. The size of this concavity seems to depend on the distance of the occipital suture from the foramen. Between the occipital foramen and the submentum are extensions of the post-genal region, which by fusion give rise to a *hypostomal bridge* which separates the submentum and the occipital foramen. This hypostomal bridge is frequently supported internally by a tentorial bridge which is associated laterally with the cornua of the occipital fold. Many cleared specimens have been prepared and illustrated and the results of these morphological studies will be embodied in a subsequent paper. A graded series showing modifications of the hypostomal bridge and the lateral extension of the occipital suture has been figured by Given (1954).

4. *The Antennae.*

In the antennae the scape and pedicel are distinct and there is a flagellum of eleven segments. In thynnids the antennae are comparatively uniform, but modifications occur in the length, breadth and perhaps the form of the segments. Above their insertions there are frontal crests or ridges which are said to be present in all the Thynnidae but absent in the Anthoboscidae.

(*a*) *Length of the antennae.*

In some examples the antennae are so long that they reach the third abdominal segment, while in others they are so short that they do not extend even to the tegulae. The length of the antennae is used as a taxonomic character in two separate sections of the generic key of 1910, and according to Turner, short antennae are a feature of *Asthenothynnus*, *Leiothynnus* and *Gymnothynnus*. To express the length of the antennae in his couplets, Turner made comparisons with the regions of the thorax; thus the extension of the antennae beyond either the pronotum, mesonotum, metanotum or the propodaeum became a convenient scale for inter-specific comparison. However, the thoracic structures are variable in length and appreciable differences exist, particularly between the proportions of both pronotum and propodaeum. Therefore, as Turner's measurements were based on a set of inconsistent standards, comparison of antennal lengths within the whole family was an impossibility and was restricted to the confines of certain groups of genera.

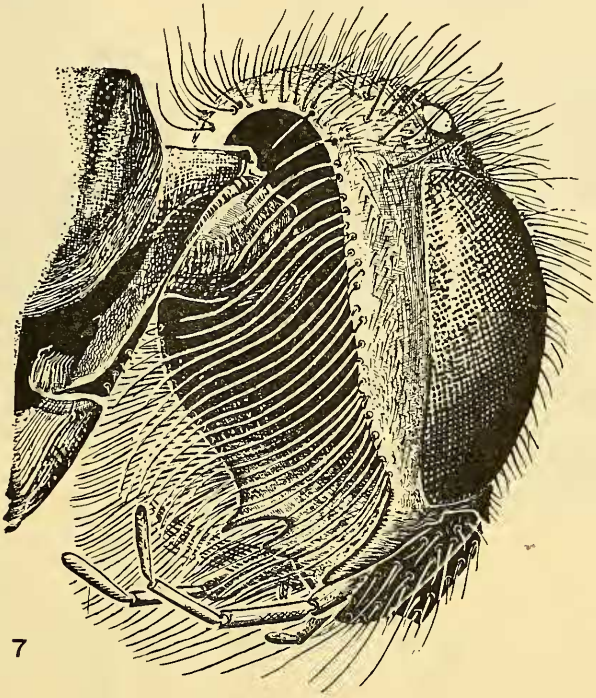
In an unidentified species of *Tachynomyia*, measuring 14 mm. in length, the antennae are 11 mm. long, while there are species of *Rhagigaster* Guérin and *Eirone* Westwood in which the antennae scarcely reach as far as the wing bases. In *Leiothynnus mackayensis* and *Gymnothynnus gilberti* the reduced antennae do not extend beyond the thoracic boundaries.

Unfortunately, in separating *Asthenothynnus* from *Neozeleboria*, Turner used the phrase "antennae considerably shorter than head, thorax and median segment combined"; however, it cannot be said that this qualification applies to all the species of *Asthenothynnus*, as was supposed; in fact, neither *Asthenothynnus lilliputianus* nor *Asthenothynnus pleuralis* conforms to Turner's characters in regard to the length of the antennae.

(*b*) *The diameter of the antennae at base and apex.*

In some species of *Hemithynnus* Ashmead, *Lophocheilus* Guérin, *Macrothynnus* Turner and *Leptothynnus* Turner, the antennae taper distally. This gave Turner yet another taxonomic character. Antennae with slenderer apices were supposed by him to distinguish *Hemithynnus* and *Lophocheilus* from one group and *Macrothynnus* and *Leptothynnus* from another.

(i) *Hemithynnus and Lophocheilus.*—The apical segments of the antennae are described as "much slenderer than basal" in *Lophocheilus* with its fourteen species, and *Hemithynnus* with twenty-four species, while by contrast the apical segments are described as "little if at all slenderer than basal" in *Thynnoides* (fourteen species), *Elidothynnus* (fourteen species), *Campylothynnus* (three species), *Lestricothynnus* (sixteen species) and *Belothynnus* (five species). Thus an attempt is made in this generic key to distinguish between a group of thirty-eight species in which the apex



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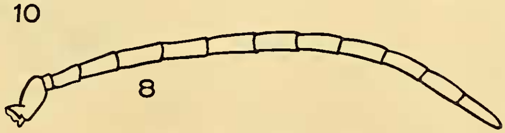

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Text-fig. 7.—*Tachynomyia adusta* (Smith). Head from postero-lateral aspect to show the occipital concavity.

Text-fig. 8.—Antenna of *Hemithynnus apterus* (Olivier), in which the apical segments are said to be much slenderer than basal.

Text-fig. 9.—Antenna of *Thynnoides fumipennis* (Westwood). In this example the apical segments are said to be "little if at all slenderer than basal".

Text-fig. 10.—Antenna of *Guerinius shuckardi* (Guérin). The phrase used here reads "antennae not slender at apex".

is supposed by Turner to be "much slenderer" and a group of fifty-two species in which the apex is said to be "little if at all slenderer". This is most confusing and in order to demonstrate the similar nature of the characters which Turner has contrasted here, the antennae of *Hemithynnus apterus* and *Thynnoides fumipennis* are illustrated (Text-fig. 8 and Text-fig. 9). It is anticipated that this character will be found to be of little value in taxonomy.

(ii) *Macrothynnus and Leptothynnus.*—"Antennae slenderer at the apex" is the taxonomic character which Turner used to separate the five species included in *Macrothynnus* Turner and *Leptothynnus* Turner from its converse: "antennae of even thickness throughout", which characterizes *Guerinius* Ashmead, *Pogonothynnus* Turner, *Zaspilothynnus* Ashmead and *Thynnus* Fabricius (see *Guerinius shuckardi* (Guérin), Text-fig. 10).

(c) *Segments arcuate.*

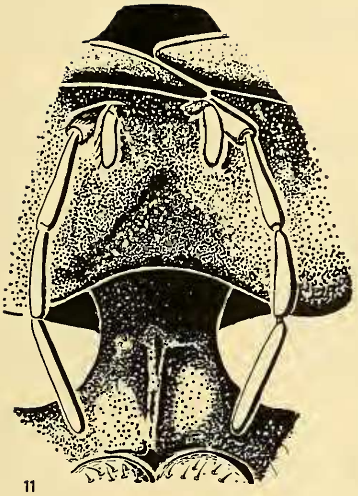
There is a tendency in some species for the long axis of each segment to become curved or arcuate. In *Phymatothynnus* Turner, "the apical joints of the antennae are very strongly arcuate", as is apparent in *Phymatothynnus nitidus.* The antennae are rather feebly arcuate in many thynnids and this character was employed by Turner to contrast the genera *Lestricothynnus* Turner and *Thynnoides* Guérin, in which the apical joints are feebly arcuate, from the genera *Belothynnus* Turner, *Elidothynnus* Turner and *Campylothynnus* Turner, in which the converse—"apical joints of the antennae not arcuate"—is used as a taxonomic character. The species thus contrasted by this character include the thirty species in *Thynnoides* and *Lestricothynnus*, which are slightly arcuate, and twenty-two in the remaining genera, which are said to be non-arcuate.

5. *The Maxillary Palp.*

There are six segments in the maxillary palp in thynnids and these segments differ in length in different genera. The relative proportions of the segments of the maxillary palp were given by Turner in his descriptions of the genera in 1910. It is presumed that his definition of each genus applied to the type species, but it is by no means certain that the segments of the maxillary palp are relatively constant within the limits of each genus, or whether these structures have any taxonomic significance at the generic level. The maxillary palps have been examined in a number of species.

There is an extraordinary contradiction in several couplets of the 1910 key regarding the use of the maxillary palp as a taxonomic character. This applies to *Ariphron* Erichson, 1842, and *Neozeleboria.* The length of the segments of the maxillary palp was used by Turner to separate *Ariphron* (Text-fig. 11) from seven other genera. In *Ariphron* "the three apical joints of the maxillary palpi are very long and slender" and contrasted with this couplet follows: "the three apical joints of the maxillary palpi not elongate or much less so". Seven genera are grouped here and, strange though it may seem, two of these, *Neozeleboria* and *Aulacothynnus*, are defined by a taxonomic character which reads: "The three apical joints of the maxillary palp moderately elongate, the fourth joint the longest." (See Text-fig. 12.) Illustrations of *Ariphron bicolor* and *Neozeleboria sexmaculata* show that there is no appreciable difference between the palps in these two species, yet their separation was attempted by these definitions in the 1910 key.

A comparison was given of the length of the segments of the maxillary palp for each genus described in the *Genera Insectorum*, 1910. In some species there are certain segments which are said by Turner to be longer than others, and an investigation was made by the present author to test the value of the information he supplied. Presuming that the description of a genus at least applies to its own type species, permanent preparations mounted in balsam were made of the maxillae of a number of examples. The dimensions of the segments of the palp were measured for a dozen different species by means of an optical micrometer, and it was very evident that significant results could only be obtained by dissecting a large series of individuals. As this was impossible, the figures obtained have not been tabulated in the present paper. Illustrations of the mouthparts, with notes on the feeding habits of certain thynnids, are supplied by Given (1954).



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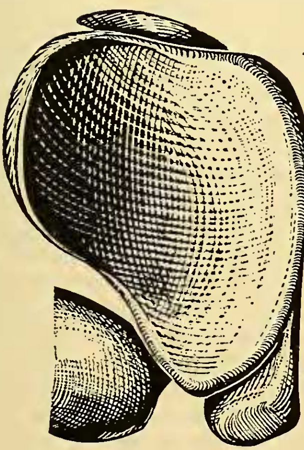

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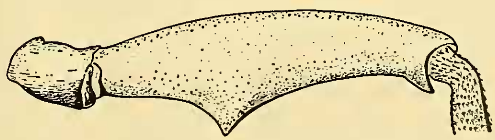

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Text-fig. 11.—Head of *Ariphron tryphonoides* (Smith), drawn from the ventral surface to illustrate the character which Turner used—"the three apical joints of the maxillary palpi very long and slender".

Text-fig. 12.—Head of *Neozeleboria sexmaculata* (Smith) drawn from the ventral surface to illustrate the taxonomic character—"three apical joints of the maxillary palpi moderately elongate, the fourth joint the longest".

Text-figs. 11 and 12 show the apex of the clypeus, the tips of the mandibles, the labial and maxillary palps, neck and the fore-coxae.

Text-fig. 13.—Right fore-coxa of *Thynnoides fumipennis* (Westwood) drawn from the ventral surface to illustrate the taxonomic character—anterior coxae very strongly concave beneath.

Text-fig. 14.—Left posterior femora of *Aulacothynnus femoratus* (Turner), which bears an extraordinary tubercle on its post-axial surface.

The Thorax.

The thorax presents a great deal of interest and a study of its comparative morphology in the type species of the genera of Thynnidae is giving some profitable results, which will be embodied in a subsequent work. Reference here is confined to the pronotum, portion of the mesopleuron, scutellum and propodaeum.

1. *The Regions of the Thorax.*

The Pronotum: The length of the median axis of this structure is variable and in some species the antero-dorsal aspect is elevated to form a transverse crest which may even be extended laterally into projections; this crest is in close proximity to the occipital region of the head.

The Mesepisternum: Contrasted with the family Pompilidae, the mesepisternum in Thynnidae, Scoliidae and their allies is not divided by the median episternal groove into "lower and upper portions" (Brues *et al.*, 1954, with modifications after Snodgrass, 1910).

The Scutellum: This sclerite may be elevated to a greater or lesser extent.

The Propodaeum: It was known to Turner as the median segment and several types can be recognized. One important variable is the length of its median axis, and this is so reduced in some species that the propodaeum forms an almost vertical wall to the thorax. In thynnids in which this structure is not excessively reduced, the propodaeum either tends to narrow gradually, thus forming a conical structure, or by contrast its sides may tend to become inflated and its shape is thus almost rounded.

2. *The Legs.*

As in Scoliidae and Tiphiidae, the legs in thynnids are not excessively elongate and the posterior femora do not extend beyond the apex of the abdomen. This is one of the many differences between the Thynnidae and the Pompilidae.

(*a*) *Anterior coxae.*

In some species the anterior coxae are flattened, while in others they are even laterally expanded. This expansion varies in extent and it would be possible to select a graded series of species to demonstrate the range of its development. In some species the coxae have a plain, flattened surface, while there are others in which the lateral expansions of the fore-coxae are only slightly developed. In others still this surface is slightly concave, while the series reaches its peak in forms in which the coxae bear deep concavities formed by the expansion and inflexion of their edges (Text-fig. 13). Turner attempted to use these coxal cavities in his generic key. The presence of such concavities in the thirty species comprising *Lestricothynnus* and *Thynnoides* (Text-fig. 13) was used to separate these two genera from the supposed absence of such cavities in the twenty-two species included in *Belothynnus*, *Elidothynnus* and *Campylothynnus*. It is worthy of note, however, that similar coxal cavities are present in genera other than *Lestricothynnus* and *Thynnoides*. The presence of coxal cavities is not limited, therefore, to the thirty species belonging to these two genera, and furthermore, on account of the intergradient nature of this taxonomic character, distinction is impossible between the sixteen species in Turner's "feebly concave" *Lestricothynnus* and the fourteen species characterized by his "very strongly concave"—*Thynnoides* (Text-fig. 13).

In species in which the fore-coxae are concave, it seems safe to assume that these saucer-like pouches, facing the mouth, would become packed with pollen and honey. As in *Tachynomyia*, with its suboccipital concavities, coxae of this pattern would provide a reservoir of food for the female partner.

(*b*) *The second pair of coxae and the mesosternum.*

The taxonomic character given by Brues, Melander and Carpenter (1954) reads: "Mesosternum with two laminae that overlie or project between the bases of the middle coxae and usually extend to the mid-line where they are separated by a median suture." This feature characterizes the families Thynnidae, Anthoboscidae and Tiphiidae (including Myzinidae), and is contrasted with the couplet, "Mesosternum simple, without appendages behind, or with the laminae reduced to a pair of minute tooth-like projections", which applies to the Sapygidae, Methocidae and the Myrmosidae.

The proximity of the second pair of coxae was used as a taxonomic character by Imms (1951). The keys given by that author state that in Scoliidae the middle coxae are widely separated, as in Brues *et al.*; in the Thynnidae the middle coxae are usually separated by a triangular or bilobed projection of the mesosternum, while Imms states that in the Myrmosidae and the Mutillidae the middle coxae are contiguous.

(*c*) *The posterior femora.*

In *Aulacothynnus femoratus* (Turner) and *Aulacothynnus calcaratus* (Smith) there is a most extraordinary spine-like outgrowth arising from the post-axial surface of the hind femora. The presence of this tubercle distinguishes *Aulacothynnus* in which only two species are recognized, from *Neozeleboria.* Specimens of *Aulacothynnus* are rarities in the collections of the museums of the Commonwealth of Australia. A spine or tubercle on the femur is distinctive in Thynnidae (see Text-fig. 14), for, although spines, ridges and crests occur elsewhere in these Hymenoptera, a femoral projection is most conspicuous. A thick stout spine is present on the post-axial surface of the femur of *Megalothynnus poultoni* (Turner), and there is a distinct prominence in *M. klugii* (Westwood), which is apparent in that author's illustrations.

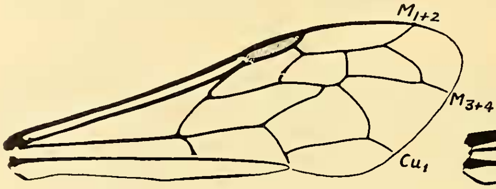
3. *The Fore–Wing.*

In general the venation in Thynnidae shows a remarkable consistency, except for minor differences in the relative dimensions of the various veins, cross-veins and cells in different species. It is probable that such minor differences could be of value at the generic and even specific level. Thynnid wing-venation has been recognized as a means of separating these insects from their allies since the days of Latrielle, Jurine and Lepeletier, and in recent works its value is still recognized. As the families Methocidae, Myrmosidae and Myzinidae are absent from our fauna, Tillyard used the extension of the wing-venation to the wing margin to separate the Australian Thynnidae from the Scoliidae and Mutillidae. One feature of particular interest is used by Brues *et al.* (1954), Pate (1947) and others; it consists of a curious little spur or veinlet which forms a small cell immediately behind the pterostigma. It is adequately described in "Histoire Naturelle des Insectes", Lepeletier de Saint Fargeau (1845), which reads: "*Caractères des ailes.* Une radiale ovale, grande. Quatre cubitales; la première séparée en deux par une nervure descendant de la côte sans atteindre le cubitus. La seconde reçoit la première nervure récurrente. La troisième cubitale reçoit la deuxième récurrente. La quatrième, assez courte, atteint le bout de l'aile."

Regarding thynnid wing-venation, there are various terminologies in use by hymenopterists. Brues, Melander and Carpenter (1954) state: "Wing-venation of male complete and extending out to the tips of the wings, three closed cubital cells, the first usually divided at least partially by a spur from the first intercubitus"; while Pate's terminology differs slightly and reads: "Fore-wings with the first submarginal cell more or less divided by a spur from the first transverse cubital vein"; and Tillyard (1926) gave the following interpretation: "The fore-wing has cells *1r* and *2r* partly united, only a small spur indicating their original separation by the cross vein rm_1 . . . ." The spur to which Lepeletier refers in 1845 was thus regarded by Tillyard as the first radio-median cross-vein rm_1 arising from near the base of his M_{1+2} and therefore, according to that worker, corresponded to the first radio-median cross-vein in *Sirex* sp. (Siricidae), a member of the Chalastrogastra, which are apetiolate Hymenoptera far removed from the Thynnidae.

Once again, *Diamma bicolor* Westwood, subfamily Diamminae, is found to differ from both the subfamilies Rhagigasterinae and the Thynninae, and it could be said that no cross-vein or spur rm_1 exists in Diamminae. However, an examination of the wings of twelve specimens shows that in eight the spur is entirely absent, while in four one or more small, fragmentary, disjointed filaments can be demonstrated, which are situated in the general position usually occupied by rm_1. Furthermore, whereas it is usual in thynnids to find that the cross-vein rm_1 arises from a kink in the first transverse cubital vein (= base of M_{1+2}), in *Diamma bicolor* the kink is absent, and is represented instead by a weakened perforation in the first transverse cubital at the point where rm_1 would be expected to arise (Text-fig. 15).

The family Vespidae may be distinguished from the Scoliidae, Thynnidae and Tiphiidae by wing-venation, and this could be of some interest, since both Tillyard



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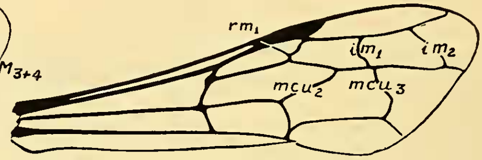

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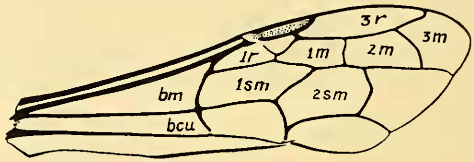

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Text-fig. 15.—Right fore-wing of *Diamma bicolor* Westwood, in which mcu_3 meets M_{3+4} on the proximal side of im_1.

Text-fig. 16.—Right fore-wing of *Oncorhinothynnus xanthospilus* (Shuckard). In this example mcu_3 and im_1 are said to be "interstitial".

Text-fig. 17.—Right fore-wing of *Epactiothynnus crabroniformis* (Smith).

Text-fig. 18.—Right fore-wing of *Thynnoides fumipennis* (Westwood).

As illustrated, it is usual to find mcu_3 meeting M_{3+4} on the distal side of im_1. However, the proximity of these two cross-veins is variable. Text-figures 17 and 18 attempt to illustrate the meaning of the couplet reading: "Second recurrent nervure received very near the base of the third cubital cell", and its converse—"Second recurrent nervure received by the third cubital cell not very near the base".

Terminology Used in Wing-venation.

	Tillyard's System.	The Jurinian and Other Systems.
M_{1+2} ..	Fused first and second median vein:	
	Basal piece.	1st transverse cubital (=1st intercubitus).
	Distal piece.	Radius.
M_{3+4} ..	Fused third and fourth median vein.	Cubital.
rm_1 ..	1st radio-median cross-vein.	Spur on 1st transverse cubital vein.
im_1 ..	1st intermedian cross-vein.	2nd transverse cubital.
im_2 ..	2nd intermedian cross-vein.	3rd transverse cubital.
mcu_2 ..	2nd medio-cubital cross-vein.	1st recurrent.
mcu_3 ..	3rd medio-cubital cross-vein.	2nd recurrent.
1r ..	1st radial cell.	1st cubital cell (=1st submarginal cell).
3r ..	3rd radial cell.	Radial cell (=2nd radial cell).
1m ..	1st median cell.	2nd cubital cell (=2nd submarginal cell).
2m ..	2nd median cell.	3rd cubital cell (=3rd submarginal cell).
3m ..	3rd median cell.	4th cubital cell (=4th submarginal cell).
1sm ..	1st submedian cell.	1st discoidal cell.
2sm ..	2nd submedian cell.	2nd discoidal cell.
bm ..	Basimedian cell.	Subcostal cell (=median cell).
bcu ..	Basicubital cell.	Median cell (=submedian cell).

and Imms (1951) classify these insects together in the superfamily Vespoidea. The couplet in Brues *et al.* (1954) reads: "First discoidal cell (= *1sm*) shorter than the submedian cell (= *bcu*)";* this includes the Tiphiidae, Thynnidae etc., and is contrasted with "first discoidal cell (= *1sm*) very long, as a rule much longer than the submedian cell (= *bcu*)", which applies to the Vespoidea. In consequence the Tiphiidae

* Tillyard's notation is given in parentheses.

and Thynnidae stand apart from the Vespidae on account of their wing-venation as well as the form of the posterior lateral lobes of the pronotum. To show the phylogenetic relationship of the families Bradynobaenidae, Myrmosidae, Anthoboscidae, Tiphiidae, Myzinidae, Thynnidae and Methocidae is most desirable (Pate, 1947); however, to achieve this, use of the taxonomic category—superfamily—seems most logical. It is suggested here that this assemblage be grouped into the superfamily Tiphioidea and thus separated from the superfamily Vespoidea.

As regards minor differences in thynnid wing-venation, one important variable is the position of the third medio-cubital cross-vein mcu_3 in relation to the intermedian cross-vein im_1, upon the vein M_{3+4}. Tillyard's interpretation is used here, and for convenience the above statement is repeated in the older notation with Tillyard's lettering given in parentheses and reads thus: "The position of the junction of the

TABLE 3.

The Dimensions of the "Cubital Nervure" ($=M_{3+4}$).

The third medio-cubital cross-vein mcu_3 is received by M_{3+4} either "very near" or "not very near" to the first intermedian cross-vein im_1. In the table that follows, the distance between the junction of im_1 and mcu_3 is given for ten examples. For comparative purposes the proximity of im_1 and mcu_3 is expressed as a percentage in relation to the distance between im_1 and im_2.

Species.	Dimensions of M_{3+4} between		Proximity Expressed as a Percentage Ratio.	Description Given in Turner's Generic Key of 1910.
	im_1 and mcu_3.	im_1 and im_2.		
	mm.	mm.	%	
Oncorhinothynnus xanthospilus ..	0·17	2·73	6	"2nd recurrent nervure interstitial with 2nd transverse cubital nervure."
Tmesothynnus zelebori	0·14	1·41	10	"2nd recurrent nervure received very near the base of the 3rd cubital cell."
Aspidothynnus rostratus	0·12	1·07	12	
Epactiothynnus crabroniformis ..	0·17	1·34	13	
Hemithynnus apterus	0·76	3·81	20	"2nd recurrent nervure received *not* very near the base of the 3rd cubital cell."
Belothynnus unifasciatus	0·76	3·21	24	
Thynnoides fumipennis	0·56	2·15	26	
Elidothynnus melleus	0·76	2·83	27	
Campylothynnus assimilis	0·7	2·55	28	
Lophocheilus villosus	1·01	2·86	35	

second recurrent vein (= mcu_3) varies in its relation to the second transverse cubital vein (= im_1) on the (so-called) cubital vein (= M_{3+4})." (Text-figs. 15–18.)

Certain variations occur in the union of the second recurrent vein (= mcu_3) with this so-called cubital vein (= M_{3+4}). These variations fall into three categories: (i) upon the proximal side of the second transverse cubital vein (= im_1) and thus on the second cubital cell (= *1m*) (Text-fig. 15); (ii) in contact with the second transverse cubital vein (Text-fig. 16); (iii) on the distal side of the second transverse cubital vein, that is by the third cubital cell (= *2m*) (Text-figs. 17 and 18). In this last instance the junction of the second recurrent vein (= mcu_3) may be either close to or some little distance from the second transverse cubital vein (= im_1).

The form taken by this second recurrent vein (= mcu_3) is of importance, as it is the principal taxonomic character which separates the subfamily Diamminae from the subfamilies Rhagigasterinae and the Thynninae. For the second cubital cell (= *1m*) to receive the second recurrent nervure as well as the first is an aberrant feature and occurs only in the monotypic *Diamma bicolor.* This feature was recognized by Shuckard (1835) in his description of *Psamatha chalybea,* which later was shown to be the male form of *Diamma.* It is the only known thynnid in which the second recurrent, together with the first recurrent (= mcu_2), is received by the second cubital cell (= *1m*), and the assignment of *Diamma* to the family Thynnidae has been questioned by Clausen (1940). Contact between the second recurrent (= mcu_3) and the second transverse cubital (= im_1) is found in the monotypic species *Oncorhinothynnus xanthospilus* (Shuckard, 1841) (Text-fig. 16). For some one hundred and twenty-eight species the distance separating the junctions of the second transverse cubital and the second recurrent nervures was used by Turner in the following couplet: "Second recurrent nervure received very near the base of the third cubital cell." This is supposed to separate *Aspidothynnus*, *Gymnothynnus*, *Epactiothynnus*, *Tmesothynnus* and *Catocheilus*, in which there are forty species from "Second recurrent nervure received by the third cubital cell not very near the base", which includes eighty-eight species in *Hemithynnus*, *Lophocheilus*, *Thynnoides*, *Lestricothynnus*, *Elidothynnus*, *Campylothynnus* and *Belothynnus*.

Unfortunately, Turner's "very near" and "not very near" are ill defined and the character intergrades over the range of some one hundred and twenty-eight species. There are many species in this group of genera, however, which cannot be placed with certainty into either division of this couplet, and thus, like so much of the 1910 generic key, it is doubtful if Turner's couplet has any real significance. Several measurements are supplied in Table 3, and illustrations are given of the wings of *Epactiothynnus crabroniformis* (Smith) and *Thynnoides fumipennis* Guérin (Text-figs. 17 and 18).

The Abdomen.

In the abdominal region there are eight segments and a hypopygium. The first segment is the propodaeum, which has already been considered with the thorax, and the second is constricted at its base to form the petiole. Thus, the gaster is composed of seven segments and, consequently, the apparent seventh segment is morphologically the eighth. At the posterior end of the ultimate sternite is the hypopygium. Between the sternites of the apparent first and second abdominal segments there is a deep groove present in Thynnidae, Myrmosidae, Mutillidae and Scoliidae. The modifications occurring in abdominal morphology may be summarized as follows: (*a*) the abdomen varies in shape, (*b*) the individual segments are variously moulded, and (*c*) spines and protuberances are present on certain segments.

(*a*) *The shape of the abdomen.*

The shape of the abdomen is far from uniform, and since there are modifications in the dimensions of the longitudinal, transverse and median vertical axes, several important taxonomic characters have been derived from its general appearance. Examples will be illustrated in a subsequent paper.

Firstly, its longitudinal axis is often elongated. Secondly, its transverse axis may be uniform throughout, or it may be narrower at both base and apex, as in the lanceolate forms, or the widest axis may be basal, as in the conical forms. Thirdly, the median-vertical axis is of much significance, as the ratio between median-vertical axis and transverse axis is such that the abdomen often has a flattened appearance. The various types of abdomen gave Turner valuable taxonomic characters which he used in his attempts to form a classification. Turner applied the taxonomic character, "abdomen flattened", to the following genera: *Ariphron*, *Psammothynnus*, *Phymatothynnus*, *Zeleboria*, *Aulacothynnus*, *Neozeleboria*, *Asthenothynnus* and *Leiothynnus*. Contrasted with this is the character, "abdomen not flattened", which naturally is applicable to the species with a cylindrical abdomen; however, in many species the abdomen is elliptical in transverse section, and thus it appears to be slightly flattened dorso-ventrally. As a consequence, Turner's expression is a little misleading.

That it is difficult to distinguish between Turner's so-called "abdomen flattened" and his "abdomen not flattened" is illustrated by Table 4. Here the dimensions of the median-vertical and transverse axes are given and the ratio is expressed as a percentage. Fourteen examples were used, and of these all but two are the type species of their corresponding genera. As usual the extremes are easily separated, but in the "flattened" group, there are a number of examples in which the median-vertical to transverse ratio exceeds even some of those which are included in the "not flattened" group. To separate all of the eighty species in the "flattened" section from the remainder by this taxonomic character is scarcely practicable.

(*b*) *The moulding of the abdominal segments.*

The abdominal segments differ in shape in different species. There are numerous examples in which each segment is uniform in diameter throughout its length, while in others the individual segments are constricted to a greater or lesser extent at each end. Such intersegmental constrictions are a feature of *Lophocheilus* and *Thynnoturneria* but they are not found in *Hemithynnus* (Text-fig. 19).

TABLE 4.

Dimensions of the Median-vertical and Transverse Axes of the Abdomen.

Turner's generic key attempts to separate approximately 80 species from 250 species by the taxonomic character " abdomen much flattened, more or less fusiform " *vs.* " abdomen not flattened ". Vertical and transverse dimensions and the percentage ratio are given in this table for 14 species. The intergradient nature of this division is illustrated by a comparison of the percentage ratio and the taxonomic character given by Turner. The species marked by an asterisk are type species.

Species.	Median-vertical and Transverse Dimensions.		Ratio of Median-vertical to Transverse Axis Expressed as a Percentage.	Taxonomic Character Implied by Turner in Generic Key of 1910.
	Median-vertical Axis.	Transverse Axis.		
	mm.	mm.	%	
*Zeleboria xanthorrhoei**	1·07	2·25	48	" Abdomen much flattened: more or less fusiform."
Phymatothynnus nitidus	1·13	2·08	54	,, ,, ,, ,,
*Aulacothynnus femoratus**	0·97	1·66	58	,, ,, ,, ,,
*Ariphron bicolor**	1·54	2·49	62	,, ,, ,, ,,
*Psammothynnus depressus**	1·5	2·39	63	,, ,, ,, ,,
*Neozeleboria sexmaculata**	1·64	2·58	64	,, ,, ,, ,,
*Asthenothynnus pulchellus**	0·81	1·22	66	,, ,, ,, ,,
*Hemithynnus apterus**	4·1	5·9	69	" Abdomen *not* flattened."
*Leiothynnus mackayensis**	1·09	1·53	71	" Abdomen much flattened."
*Guerinius flavilabris**	4·06	5·5	74	" Abdomen *not* flattened."
*Thynnoturneria cerceroides**	1·13	1·52	74	,, ,, ,,
Thynnus pulchellus	3·7	4·84	76	,, ,, ,,
*Zaspilothynnus leachiellus**	3·65	4·27	85	,, ,, ,,
*Agriomyia maculata**	2·63	3·04	87	,, ,, ,,

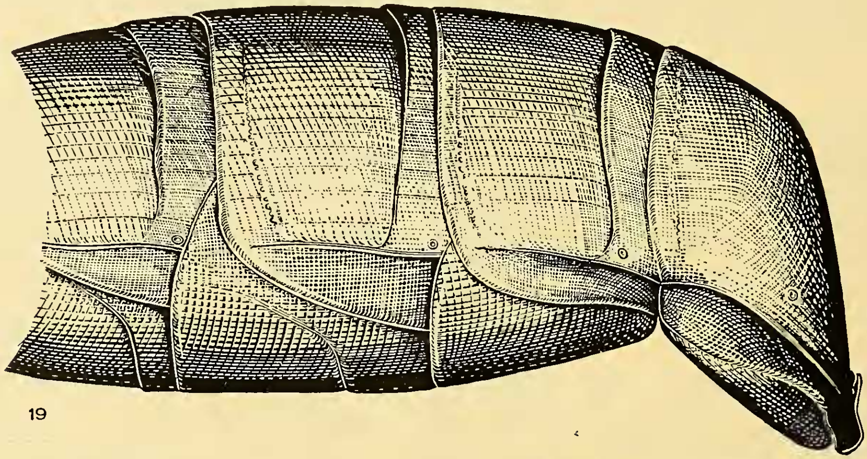
(*c*) *Abdominal protuberances.*

In some species tubercles are present on the sternites. These ventrally situated tubercles may be (i) median or (ii) ventro-lateral. A median tubercle may occur on the apparent first abdominal sternite and sometimes upon the anterior margin of the apparent second sternite. There are several species which have paired, rudimentary tubercles on the third and fourth sternites, while on the apparent fifth and/or sixth sternite paired tubercles sometimes occur. There is a group of thynnids which have a transverse crest on the pygidium.

(i) *The median tubercle.*—That the first abdominal sternite is always separated from the second by a deep groove is a taxonomic character appertaining to all Thynnidae. As a consequence, in many species the first sternite becomes conical or pyramidal in shape. In *Agriomyia* and *Belothynnus* the apex of this prominent structure is produced into a thin spine-like projection which forms an obvious tubercle. In *Agriomyia,* this tubercle forms a straight, cylindrical projection, while by contrast, in *Belothynnus* it is curved posteriorly (Text-fig. 20, 21).

(ii) *Projections borne by the postero-lateral aspect of certain sternites.*—Tooth-like projections are borne on the postero-lateral aspect of certain sternites. These projections are paired and arise either as posterior extensions of transverse sternal ridges or as tubercles on the postero-lateral aspect of the sixth sternite.

The abdominal segments are constricted in many thynnids at their intersegmental junctions; thus the central region becomes elevated. In some species this elevated portion gives rise to a transverse ridge which sometimes appears on each segment. Such transverse ridges are formed on the sternites of *Thynnoturneria* Rohwer, a genus comprising twenty-two species. In some forms the postero-lateral aspect of these



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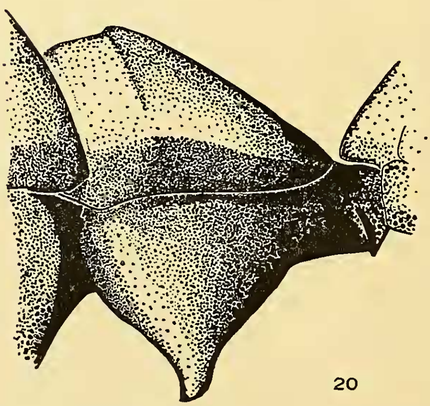

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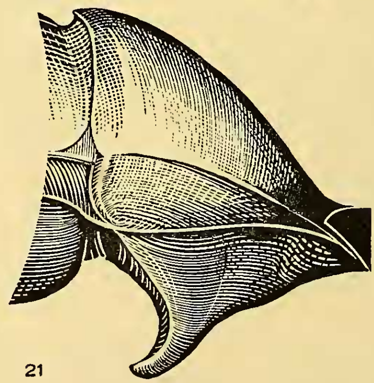

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Text-fig. 19.—Anterior portion of the abdomen of *Hemithynnus apterus* (Olivier). This shows Turner's "abdominal segments very slightly or not at all constricted", and also the groove which divides the first and second abdominal sternite.

Text-fig. 20.—First abdominal sternite of *Agriomyia maculata* Guérin to illustrate Turner's "first ventral segment with a vertical tubercle near the middle".

Text-fig. 21.—First abdominal sternite of *Belothynnus impetuosus* (Smith), illustrating the meaning of "first ventral segment with a tubercle at the apex".

transverse sternal ridges bear sharp cusps. These cusps reach their maximum development in the five species included in *Acanthothynnus* Turner and *Doratithynnus* Turner (Text-fig. 23), and the presence of "a very long stout spine at the apical angles of the fifth ventral segment" was the taxonomic character used in 1910 to separate these two genera from *Thynnoturneria*. In *Thynnoturneria* (Text-fig. 22) there is a tooth-like structure developed on the postero-lateral aspect of the sixth sternite, but in this case the fifth sternite is unarmed.

This tendency to form a projection on the postero-lateral aspect of the abdomen is not limited to *Thynnoturneria*. A pair of spines is present on the postero-lateral aspect of the sixth sternite in *Leptothynnus*, *Pogonothynnus*, *Zaspilothynnus* (Text-fig. 25) and *Thynnus*, which is a valuable taxonomic character. It is not a feature which is related to the constriction of the segments as in *Thynnoturneria* and, furthermore, it is only present on the sixth sternite, never on the fifth. There is little resemblance between the spine in this group and the tooth-like structure of *Thynnoturneria*. Spines do not occur on the sixth ventral segment in *Macrothynnus* (Text-fig. 24).

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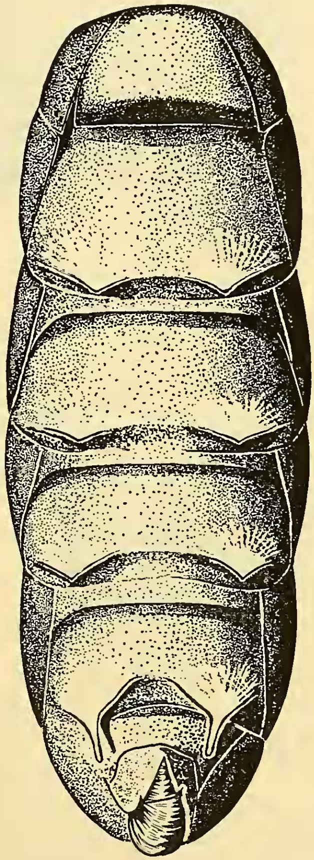

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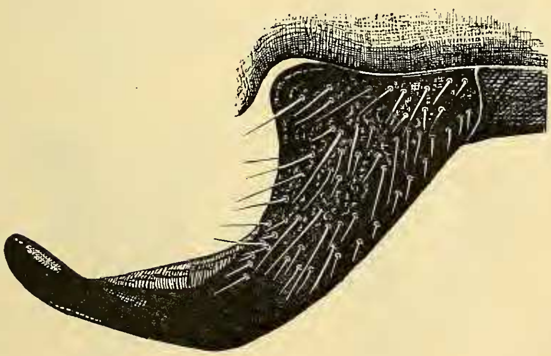

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Text-fig. 22.—Posterior extremity of *Thynnoturneria cerceroides* (Smith) from the lateral aspect, showing the short spine at the apical angle of the sixth sternite and the absence of a spine on the fifth.

Text-fig. 23.—Entire ventral surface of *Doratithynnus doddii* (Turner), in which long stout spines occur at the apical angles of the fifth sternite and no spines are found on the sixth.

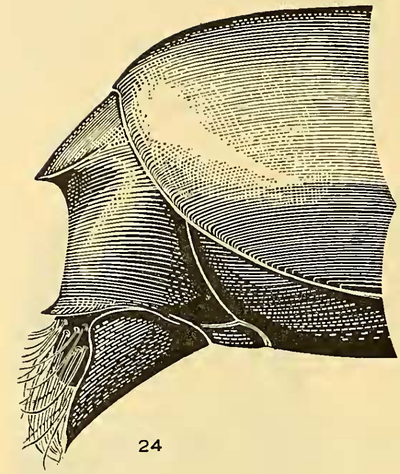
Text-fig. 31.—*Megalothynnus klugii* (Westwood). Hypopygium from lateral aspect, showing the strongly recurved blunt process.

(*d*) *The pygidium.*

There is a tendency in some thynnids for the pygidium to be produced backwards into a flattened plate-like crest, which is sometimes associated with a series of transverse striae. The striae are present in *Megalothynnus* but there is no crest, while crests are developed to a varying extent in *Macrothynnus* (Text-fig. 24), *Leptothynnus*, *Guerinius*, *Pogonothynnus*, *Zaspilothynnus* (Text-fig. 25) and *Thynnus*.

(*e*) *The hypopygium.*

The abdomen terminates ventrally in a flattened plate lying immediately below the genital opening. This varies considerably in shape in different species and, as in



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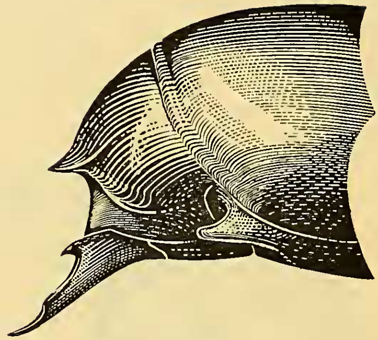

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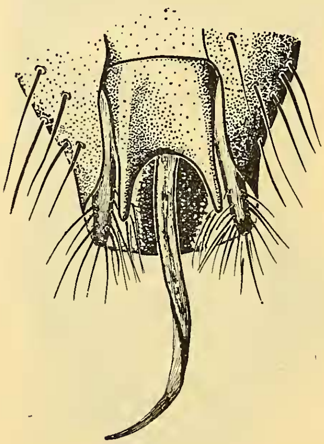

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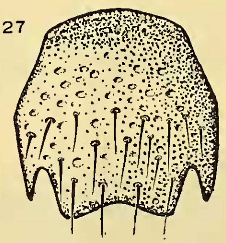

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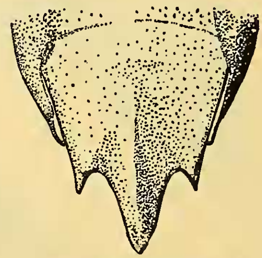

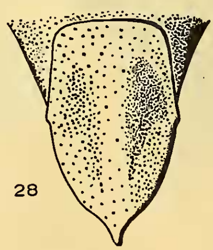

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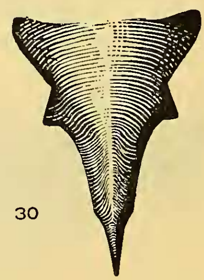

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Text-fig. 24.—*Macrothynnus simillimus* (Smith).

Text-fig. 25.—*Zaspilothynnus leachiellus* (Westwood).

The pygidium bears a dorsal crest in each species. *Zaspilothynnus leachiellus* bears a tubercle on the postero-lateral aspect of the sixth sternite and by contrast the sixth ventral segment is without a spine in *Macrothynnus simillimus*. Two forms of hypopygium are also illustrated.

Text-fig. 26.—*Psammothynnus depressus* (Westwood), in which the phrase used reads: "hypopygium emarginate, with a pointed spine on each side at the base and a tuft of hairs".

Text-fig. 27.—Hypopygium of *Zeleboria xanthorrhoei* (Smith), which is emarginate and lacks an apical spine.

Text-fig. 28.—*Neozeleboria sexmaculata* (Smith), showing a type which is longer than broad and is armed with a short apical spine.

Text-fig. 29.—Hypopygium of *Ariphron tryphonoides* (Smith), which is tridentate.

Text-fig. 30.—Hypopygium of *Guerinius shuckardi* (Guérin), showing lateral "shoulder-like" formations about halfway along the median protuberance.

other regions of Thynnid anatomy, this sclerite has the natural tendency to give rise to angular outgrowths and spines. There are examples of single-spined, bifid, tridentate and even penta-spinous hypopygia and in some species the hypopygium bears a large prominent spine on its ventral surface. Much importance was attached to this structure by Turner and, as there are many different forms of hypopygium, it has been used extensively in taxonomy.

In the subfamily Diamminae it is rounded and by contrast in some of Turner's Rhagigasterinae this structure is armed with a long, recurved, ventral spine. The hypopygium in the subfamily Thynninae shows great diversity of form and the tendency towards spinescence is displayed in many species. There are species in which the hypopygium is devoid of spines and is rounded while, by contrast, there are many others with hypopygia bearing one or more spines. Its value, however, as a taxonomic character remains as yet to be tested over large series of specimens.

There are species in which the basal spines are accentuated and the median spine is absent; this type of hypopygium is well illustrated by *Psammothynnus depressus* (Text-fig. 26), which has long, lateral spines separated by a deep incisure. By contrast, the lateral spines are relatively inconspicuous cusps arising close to the base of a median emarginate structure, as in *Zeleboria xanthorrhoei* (Text-fig. 27).

Differing completely from the preceding examples are hypopygia in which the median axis is accentuated and the outline of this sclerite is basically triangular. A simple illustration of this type of hypopygium is *Neozeleboria sexmaculata* (Text-fig. 28), in which the hypopygium narrows towards the apex to form an acute angle and there is also a slight tendency towards spinescence at its base. There are very many examples of hypopygia which are triangular in form; however, its triangular outline may be obscured owing to the rounded nature of its sides and its central spine may be developed to a varying degree. Instead of being rounded, the sides of the triangular hypopygia may curve inwards to a greater or lesser extent, thus tending to emphasize the median spine.

One modification of this elementary triangular form is illustrated by *Ariphron tryphonoides* (Text-fig. 29), in which the basal spines have become accentuated, thus giving the hypopygium a tridentate appearance. The median spine or protuberance is not accentuated here; however, there are numbers of modifications and in particular the median protuberance is often relatively elongate and expanded basally, and a series of species could be selected and arranged in order illustrating the progressive development of an additional pair of spines on the hypopygium. These spines arise on the sides of the median protuberance and together with the basal and apical spines the hypopygium becomes penta-spinous (Text-fig. 30).

The first step in the development of a five-spined from a three-spined hypopygium is the appearance of lateral "shoulder-like" formations about halfway along the median protuberance. These shoulders result from the uneven nature of the tapering of the median protuberance. Instead of it gradually narrowing to a point, the width of the median protuberance may decrease abruptly, to terminate either in a triangular apex or in a narrow, acute spine, as in *Guerinius shuckardi* (Text-fig. 30). These shoulders in such hypopygia are often produced to varying degrees to form the additional pair of lateral spines occurring in penta-spinous hypopygia, as in *Thynnus dentatus* Fabricius. In *Megalothynnus*, which has a striated pygidium, the hypopygium ends in a strongly recurved blunt process (Text-fig. 31).

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